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Journal

Current zoology, 62(1)

ISSN

1674-5507

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Publication Date

2016-02-01

DOI

10.1093/cz/zov006

Peer reviewed

Current Zoology, 2016, 62(1), 39–44
doi: 10.1093/cz/zov006
Article

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Spearfishing-induced behavioral changes of an unharvested species inside and outside a marine protected area

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Received on 29 October 2014; accepted on 7 April 2015

Abstract

By prohibiting fishing, marine protected areas (MPAs) provide a refuge for harvested species. Humans are often perceived as predators by prey and therefore respond fearfully to humans. Thus, fish responses to humans inside and outside of an MPA can provide insights into their perception of humans as a predatory threat. Previous studies have found differences in the distance that harvested species of fish initiate flight (flight initiation distance—FID) from humans inside and outside an MPA, but less is known about unharvested species. We focused on whether the lined bristletooth *Ctenochaetus striatus*, an unharvested surgeonfish, can discriminate between a snorkeler and a snorkeler with a spear gun inside and outside of a no-take MPA in Mo'orea, French Polynesia. Additionally, we incorporated starting distance (the distance between the person and prey at the start of an experimental approach), a variable that has been found to be important in assessing prey escape decisions in terrestrial species, but that has not been extensively studied in aquatic systems. Lined bristletooth FID was significantly greater in the presence of a spear gun and varied depending on if the spear gun encounter was inside or outside of the MPA. These results imply a degree of sophistication of fish antipredator behavior, generate questions as to how a non-targeted species of fish could acquire fear of humans, and demonstrate that behavioral surveys can provide insights about antipredator behavior.

Key words: fear, flight initiation distance, learning, marine protected area, spearfishing, starting distance.

Humans impose predation threats that fish can learn about through both large-scale commercial fisheries and smaller-scale artisanal fishing. Fish may differentiate and modify their behavior when they are exposed to different fishing methods. Studies of captive fish have shown that they may have learned to avoid a dip net (Yue et al. 2004). Therefore, it is likely that fish can learn the threat of larger nets used by humans in their natural habitats. Similarly, when assessing the side effects of catch-and-release fishing, catchability decreased because fish that had formerly never seen a hook learned to avoid it (Beukemaj 1970; Askey et al. 2006). Conversely, fish never exposed to fishing do not exhibit these antipredatory behaviors. This shows that fish may be more naive in areas that are protected from fishing, even if only protected periodically, and on relatively short time scales (Januchowski-Hartley 2011). Fish antipredator behavior may thus help identify fishing-induced changes in behavior. Changes in behavior, such as initiating flight earlier from a threat, may have deleterious effects on individual fitness (Ydenberg and Dill 1986), if early flight reduces foraging success.

Marine protected areas (MPAs) are implemented to manage human fishing practices and to protect fish populations (Agardy 1994) and marine communities. Fish are protected from human predation within the boundaries of a no-take MPA. However, fish may

disperse widely throughout their habitat, potentially diminishing the effects of MPAs (Gaines et al. 2010).

Protection from fishing can have direct effects by reducing mortality of harvested species or indirect effects by inducing behavioral changes in marine animals. Predator-generated behavioral changes may alter the spatial distribution of herbivores by altering foraging behavior (McCormick and Manassa 2008) because prey will spend less time foraging in risky patches (Frid and Dill 2002). Behavioral effects are expected to be strongest if a fish's range lies entirely within or outside an MPA. If protection is absolute, fish that do not range widely should respond to humans and human-associated fishing differently inside and outside of an MPA (Januchowski-Hartley et al. 2013). By assessing the difference in behavior of fish inside and outside of an MPA, we can acquire a better understanding of human-induced effects on marine ecosystems.

In Pacific Island countries and territories, spearfishing is an important form of artisanal fishing but is relatively less regulated than on islands in the Caribbean and Indian Ocean (FAO 2006; Gillet and Moy 2006). Spearfishing results in less bycatch and its direct effects are consequently focused on harvested species. However, the indirect effects exhibited by behavioral changes in fish may not be restricted to only species that are targeted. Predator avoidance can be learned socially from conspecifics and heterospecifics so that individuals that have never had experience with a predator can indirectly learn to avoid them (Griffin 2004). In addition, it has been found that fish in areas of lower predator density may be bolder and more willing to travel a farther distance from shelter (Madin et al. 2010). Though previous studies have not found a significant effect of the presence of a spear gun on fish behavior (Januchowski-Hartley et al. 2012b), acknowledging the complexity of fish behavior in response to predation, we sought to further investigate this question. By capitalizing on the selectivity of spearfishing, we can acquire a better understanding of the behavioral changes caused by human presence and how this extends to a fish species that is not directly targeted.

Flight initiation distance (FID), the distance a prey species will allow a predator to approach before fleeing (Ydenberg and Dill 1986) can be used to study how species' perceive human activities (Price et al. 2014), and thus can be used to determine how risky a fish perceives a human-related stimulus to be. All else being equal, the greater the level of risk perceived by the fish, the greater the expected FID (Stankowich and Blumstein 2005). Studies in terrestrial systems have shown that starting distance plays a large role in FID because the farther a predator is from the prey, the more time the prey has to become alert to the presence of the predator (Blumstein et al. 2004; Cooper 2005). Animals may generally initiate flight soon after they become alert to avoid the attentional costs of monitoring the predator as it approaches (Blumstein 2010; Samia and Blumstein 2014). Accordingly, an animal will flee as soon as it detects the predator to avoid such costs, so a longer starting distance means an earlier detection distance and subsequently, a longer FID. Thus, if there is variation in starting distance, this variation must be considered when trying to explain variation in FID.

Previous studies assessing fish FID in and around MPAs found no effect of dive gear (snorkel or SCUBA), or the presence of a spear-gun mimic (Januchowski-Hartley et al. 2013). A growing literature on the response of fish to spearfishing indicates that fished species can at least distinguish the threat of humans in unprotected areas (Gotanda et al. 2009; Feary et al. 2011; Januchowski-Hartley et al. 2012a). However, the complexity of this response is not yet fully understood. Additionally, studies conducted to date have not included starting distance as an important covariate, a factor that is known to influence the FID in other taxa (Blumstein 2010).

We focused on lined bristletooth, *Ctenochaetus striatus* (Acanthuridae), a surgeonfish, to understand how fish not targeted by spear fishers might respond to spear guns inside or outside of an MPA, and to assess the effects of heterospecific learning in response to predators. Lined bristletooth are an ideal species to study for a number of reasons. First, they have relatively small home ranges. The home range size in the Red Sea averages 12.1 m^2 (range: 5.8–16.4 m^2) (Krone et al. 2008). The feeding area among individuals in the southwest Indian Ocean was <40 m^2 (Robertson and Gaines 1986). Furthermore, they have not been reported to move much between foraging and spawning sites (female median distance = 80 m; male median distance = 23 m, Claydon et al. 2012). With an area of 0.578 km^2 (Leoture D, personal communication), the MPA that we studied spans a much greater area than the range of the lined bristletooth. Thus, one would expect behavioral effects of the MPA on this species to be pronounced. Because the small home range of the lined bristletooth is enclosed within this MPA, we are able to assess the behavioral effects on an un-fished species with supposedly absolute protection. Second, lined bristletooth are diurnal (Montgomery et al. 1989), and thus it is relatively straightforward to quantify FID. In addition, this species is also one of the most common reef fish off the island of Mo'orea (Arias-Gonzalez et al. 1993), further increasing their accessibility. Though lined bristletooth are fished in some regions (Choat et al. 2012), those areas are reported to have relatively low incidences of ciguatera poisoning (Skinner et al. 2011). French Polynesia has relatively higher rates of ciguatera poisoning than areas in which lined bristletooth have been documented as targeted species (Skinner et al. 2011; Choat et al. 2012). Local spear fishers and residents told us that lined bristletooth are not targeted around our study sites because of the risk of ciguatera poisoning.

Materials and Methods

Study site

We measured FID of lined bristletooth inside and outside the Pihaena marine protected area (MPA) along the coast near the University of California Gump Research Station in Mo'orea, French Polynesia (17°S, 149°W). The habitat inside and outside of the MPA was not noticeably different and consisted of degraded coral patches with varying amounts of macroalgal cover. This MPA was established on 22 October 2004, covers ~662 linear meters of coastline, and has an area of 0.578km^2. We studied fish FID with and without a spear gun, inside and outside of the MPA, from 25 January 2014 to 3 February 2014, between 0730 h and 1730 h. During our time collecting data (25 h inside the MPA, 12 h outside the MPA), only 3 other snorkelers were seen within the MPA. On several occasions we saw fishing boats, and colleagues had occasionally seen spear fishers within the MPA at other times of the year, but it is not clear if these individuals were actively fishing, and the intensity of fishing was higher in nonprotected areas regardless. We used 2 treatments: a snorkeler and a snorkeler with a wooden, 160 cm long, spear gun with a white pistol grip, in which the spear was removed for safety reasons and to not violate regulations of the MPA.

Experimental procedures

Three people collected data together. The first observer, constant throughout the experiment, was snorkeling and identified target individuals (mean subject size of all trials: range: 15.24–22.86 cm;

mean ± *SD*: 18.79 ± 4.07 cm) in order to obtain FID estimates. Prior to approach, all subject fish exhibited normal, relaxed behavior, defined as neither being alert to the presence of observers, nor responding to a predator. To calculate FID, the first observer approached the subject fish from the surface at a constant velocity (mean ± *SD* of 8 pretest training trials: 1.09 ± 0.07 m/s) to imitate the effect of surface snorkeling or spearing. Velocity of predator approach can influence FID (Stankowich and Coss 2006); thus, the snorkeler's velocity was standardized throughout all trials. From the fishes' perspective, a snorkeler approaching on the surface is a tangential approach (Blumstein et al. 2004). Most terrestrial species associate higher risk with a direct approach than a somewhat indirect, tangential approach (Stankowich and Blumstein 2005). We calculated FID-direct using the Pythagorean Theorem with the measured fish depth and horizontal distance from the fish so as to know the direct distance we were from the subjects.

The snorkeler began the observation as soon as the unalerted fish was close enough to be identified. This allowed for FID to be measured from variable starting distances. Because starting distance has a general effect on FID, we measured starting distance in each trial in order to account for its effect on FID. From this starting distance and measured fish depth, which was estimated by evenly spaced marks on the weighted marker, we calculated the direct distance we began swimming toward the fish (i.e., starting distance-direct) using the same method as FID-direct. For experimental approaches with the speargun, the speargun was held parallel to the body with the tip positioned 38 cm past the snorkeler's head. The fish was considered to have fled if it moved away from the snorkeler at an increased speed (Gotanda et al. 2009), or if we noted a sudden change in direction. Most of the fish fled to open water away from the snorkeler, whereas a few fish fled toward cover. The snorkeler marked her starting position and the distance at which the fish fled by dropping a weighted marker below her shoulders. A third marker was placed below the fish's initial position and this position was verified by a second observer, also snorkeling, >10 m away. These distances were then measured, with the help of the second observer, to the nearest centimeter using a tape measure. The third observer was on a kayak and she recorded GPS locations, carried materials, and recorded data. The kayak was always >20 m from the starting point. Using the GPS coordinates, we categorized whether a trial was conducted inside or outside of the MPA.

To avoid sampling the same area multiple times in one day, we kayaked to one spot and then moved along the coast from that point. We moved on so as to assume we sampled different individuals after each test. However, some locations had more fish than others. We did not conduct experiments after seeing a predator. Areas were avoided if there was <10 m visibility, and all data were collected when it was not raining. Subject fish were tested at a maximum water depth of 2.3 m and a minimum water depth of 0.5 m (mean ± *SD*: 1.29 ± 0.43 m).

Many other factors may influence FID. Prey length—which may reflect vulnerability (Gotanda et al. 2009)—was estimated by a single person using known size objects put into the environment by another observer (4.9 ± 5.4%, average percent error ± standard deviation, $n = 12$ estimates). The distance to protective or obstructive cover (Dill and Houtman 1989; Grant and Noakes 1987), such as a coral head, was measured to the nearest centimeter (mean ± *SD*: 41.6 ± 41.4; range: 2.54–195.58 cm). Group size was defined as any individual within five body lengths and moving in the same direction (Gotanda et al. 2009); we quantified conspecifics (mean ± *SD*: 0.33 ± 0.62; range: 0–2) and heterospecifics (mean ± *SD*: 0.37 ± 0.903; range: 0–5) separately.

Statistical analysis

FID data were analyzed by fitting a three-way, general linear model. FID-direct was the response variable, with starting distance-direct as a numeric, and treatment (speargun or no speargun) and location (inside or outside of the MPA) as factors. Two-way interactions were fitted between treatment and location, starting distance-direct and location, and starting distance-direct and treatment. The three-way interaction was also fitted and would reveal if being inside or outside of an MPA significantly influenced the way fish responded to a spear gun after controlling for variation accounted for by starting distance.

We used *t*-tests to determine if covariates were significantly different as a function of location (inside/outside of MPA), or as a function of the experimental treatment (speargun/no speargun). Distance to cover, number of heterospecifics, and number of conspecifics did not differ significantly inside or outside of the MPA ($P = 0.547$, $P = 0.580$, and $P = 0.684$, respectively), or in the presence of absence of a speargun ($P = 0.679$, $P = 0.869$, and $P = 0.192$, respectively). However, fish were significantly longer inside of the MPA than outside ($P = 0.004$), but size did not vary significantly by treatment ($P = 0.622$). We thus added subject length to the model as a main effect and as a two-way interaction with location, and found that the model's main conclusions were identical.

Models were fitted in R version 3.0.2 (R development team) using the Deducer package (Fellow 2012) and in SPSS 21.0 (IBM, Armock, NY, USA). Throughout, we interpret *P*-values <0.05 as significant, report adjusted R^2 values, and use partial eta-square values as a measure of effect size. We tested for homogeneity of variance using Levene's test and failed to reject the hypothesis of homogeneous variance across treatment ($P = 0.147$).

Results

We sampled a total of 63 lined bristletooth: 24 inside the MPA without a spear, 15 inside the MPA with a spear, 10 outside the MPA without a spear, and 14 outside the MPA with a spear. The model explained 43% of the variance in FID. We found a significant main effect of starting distance (Table 1); fish initiated flight at greater distances with increasing starting distance. The main effect of starting distance had the single largest effect size estimate. In addition, there was a significant main effect of treatment. The FID of subjects was longer in the presence of a snorkeler with a speargun than when the snorkeler approached without a speargun (Table 1).

Table 1. Results from 3-factor ANOVA for response variable: FID-direct

Effect	*F*	*P*	*Partial Eta Squared*
Corrected model	7.689	<0.001*	0.495
Intercept	1.254	0.268	0.022
Starting distance-direct (SD)	22.042	<0.001*	0.286
Treatment (T)	4.654	0.035*	0.078
Location: Inside or outside of MPA (L)	0.104	0.749	0.002
SD × T	1.966	0.166	0.035
T × L	6.329	0.015*	0.103
SD × L	0.273	0.603	0.005
SD × T × L	6.152	0.016*	0.101

Significant effects ($P < 0.05$) are marked with asterisk.

There was a significant two-way interaction between treatment and location: fish approached outside the MPA without a spear permitted closer approach. We also found a significant three-way interaction (Table 1), which showed that the expected relationship between starting distance and FID was influenced by both location (inside or outside the MPA) and treatment (speargun or no speargun). Outside of an MPA, without a speargun, FID increased as the starting distance increased, showing that fish in these areas were more responsive to the presence of a speargun. Conversely, trials outside the MPA with a speargun, showed a relatively stable FID for any given starting distance (Figure 1A). Inside of the MPA, an increase in FID was seen in trials with and without a speargun (Figure 1B). Trials with a speargun inside the MPA show a more rapid increase in FID as starting distance increased than those done without a speargun (Figure 1B).

One observation, of an experimental approach without a spear of a fish outside the MPA, appears to be an outlier in that starting distance was much longer than the other experimental approaches. While we have no reason to remove this outlier, fitting a model without the outlier eliminates the significant three-way interaction. The effect of starting distance remained, and a significant interaction between location and starting distance emerged: fish outside the MPA permitted closer approach for a given starting distance.

Discussion

This is the first study of a fish to document a significant relationship between starting distance and FID. A previous study (Miller et al. 2011) of 3 different species of parrot fish ($n < 7$ ID per species) found no effect of starting distance (SD) on FID but this study was slightly confounded because not only did it include 3 different species, the body lengths of individuals varied a lot. Other studies have acknowledged that SD might be important but have controlled for it in their experimental approaches (e.g. Januchowski-Hartley et al. 2011). Because of its widespread importance in other taxa (Blumstein 2010; Samia et al. 2013), starting distance should be incorporated as a potential factor that influences the response to treatments in future studies of fish FID.

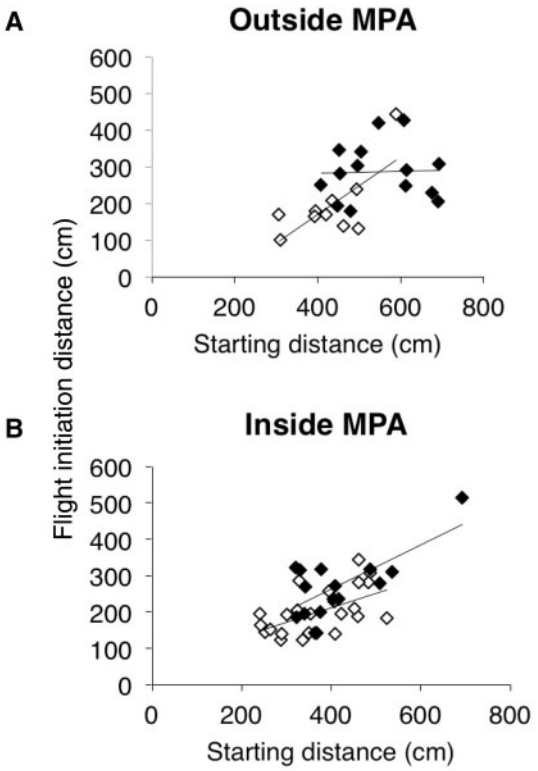

Figure 1. FID in cm as a function of starting distance, and whether the snorkeler approached with a spear (black diamonds) or without a spear (white diamonds). (A) Outside; (B) inside a MPA.

We found a significant effect of treatment on explaining FID both directly and through two-way and three-way interactions, but unlike results from recent literature (Feary et al. 2011; Januchowski-Hartley et al. 2012a, b; Januchowski-Hartley et al. 2013), we found no significant main effect of location. However, through two-way and three-way interactions we could identify the conditional effect of location on explaining variation in FID. We caution that our results are potentially driven by a single observation collected outside the MPA, but we can find no logical or methodological reason to exclude this outlier. Thus, the following interpretation should be viewed with some degree of caution and more replication, both with this species and other species, is clearly warranted.

We found that lined bristletooth initiated flight at significantly greater distances when approached by a snorkeler with a speargun than when approached by a snorkeler without one. This suggests that lined bristletooth are potentially able to recognize and respond to the threat of a speargun and differentiate this from the less-threatening presence of a human snorkeler. Proximately, this could result from fish responding to the closest object associated with the human—a spear is closer than a head. Interestingly, this discrimination ability persisted within the MPA. Notably however, outside the MPA, regardless of starting distance, lined bristletooth stayed ~3 m away from a snorkeler with a spear. Through informal conversations with island fishermen we were told that the range of a speargun could be anywhere between 1.5 m and 4 m. This finding is consistent with the hypothesis that lined bristletooth learned to remain outside the critical range of a spear gun. A difference in response to a snorkeler with a spear gun inside and outside the MPA could be explained by an enhanced response to predators with increased experience (Leahy et al. 2011) outside of the MPA. Fish not protected by the MPA would have more experiences with spear fishers and would therefore have more developed fear responses.

Unharvested species are not expected to respond to human presence because they should not identify humans as predators. However, lined bristletooth not only responded to the presence of the speargun, but specifically to the speargun inside and outside of the MPA in a way that might be expected by a fished species. They fled at greater distances to approaches with a spear gun in the relatively safer MPA, and seemingly maintained an absolute escape distance threshold in the relatively more dangerous areas outside the MPA. This is in contrast to what was previously reported from the Philippines, where a non-targeted family, Chaetodontidae, did not change its FID across reserve boundaries (Januchowski-Hartley et al. 2012a).

The ability of an unharvested fish species to learn from harvested heterospecifics may provide an explanation as to how lined bristletooth respond to humans. Social learning in shoals, prompted by chemical and visual cues, can occur between heterospecifics and can aid in the recognition of novel predators and alarm cues (Griffin 2004; Ferrari et al. 2010). Outside of the MPA, lined bristletooth are more exposed to spear fishers, and because of these additional encounters, lined bristletooth may have learned the optimal distance to maintain between themselves and a spear fisher even though they may not be directly targeted. It is also possible that they may have

learned to recognize spear fishers directly because of direct aversive encounters with spears.

Paradoxically, despite being an unharvested species, lined bristletooth behavior was distinctly different inside or outside of the MPA. Though there was occasional fishing activity observed inside of the MPA, the varying reaction of fish suggests that the fishing pressure and speargun exposure is different inside and outside of the MPA. If lined bristletooth are able to learn from heterospecifics, it is possible that fish with larger home ranges extending beyond MPA boundaries respond fearfully to the spearguns and the fish may then learn that a speargun is harmful and threatening, even if they have never had a negative experience with one. Fish learn quickly, and it may only take one experience for them to associate a speargun with a threat (Ferrari et al. 2005). Because spearguns are rare on the MPA, once this antipredator behavior is learned it is unlikely that the fish will be reconditioned to know that the speargun is not a threat (Marks and Tobeña 1990). Additionally, fish have been found to lose wariness of a threat over time if not exposed to it (Januchowski-Hartley et al. 2013). Thus, this aversion to spearguns could have been maintained through interactions with other fish or from periodic encounters with spearguns.

Aside from learning from other individuals, the presence of the speargun itself could be threatening. The speargun could be perceived as an extension of the snorkeler's body, and thus make the snorkeler seem larger, and more threatening (Helfman 1989). In swordtail fish *Xiphophorus helleri*, females used a body extension from the male's tail to assess body size (Rosenthal and Evans 1998). It is plausible that other fish species may assess body size in the same way. Future experiments should evaluate this hypothesis directly. Regardless, this mechanism provides a means to assess greater risk from a snorkeler with a spear.

Assuming that fish learn through specific chemical or visual cues of a predatory threat, our results suggest that the Pihaena MPA may not be as strictly regulated as those MPAs studied previously. Although the connectivity of marine system makes it difficult to have clear MPA boundaries (Botsford et al. 2009), if lined bristletooth protection were complete we would expect a greater difference of their behavior inside and outside the MPA. Some fish species will cross the boundaries no matter how heavily regulated it is and experience varying amounts of fishing pressure.

The difference in lined bristletooth behavior in a protected and unprotected area shows that human predation from spearfishing has an impact on marine systems via indirect reactions from nontargeted species. Although the threat from spear fishers does not impact lined bristletooth mortality, their propensity to flee earlier may result in lowered fitness (Ydenberg and Dill 1986). In a visual assessment of reef islands, the absence or presence of a distinct halo of reduced algal cover was used to infer the presence of higher trophic predators and their effect on the spatial distribution of their prey (Madin et al. 2011). By exerting top-down control and modifying fish behavior, humans could have a similar effect on prey fish species, both harvested and unharvested. Future studies at more MPAs and with more species will be needed to better understand the impact of spearfishing on marine ecosystems.

Acknowledgments

We thank the UCLA Office of Instructional Development, and the Department of Ecology and Evolutionary Biology for partial support. We thank F. and H. Murphy and the rest of the staff at the UC Berkeley Richard B. Gump Research Station for logistical support, P. Fong, C. Fong, and M. Gray for help with fish identification and N. Munoz for help with data analysis. We thank D. Leoture and the members of the PGEM association for information regarding the Pihaena MPA. Finally, we thank D. Samia, J. de Anchieta, Don Kramer, and two anonymous referees for comments on a previous version of our article.

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